

REFLECTIONS

BY

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In retrospect, I believe I had a good education for a career in coral biology: none. My Honors thesis was on the behavior of gliding possums, my Masters was on temperature regulation in lizards, and my Doctorate was on the neurophysiology of dragonflies. I have never attended a single lecture on marine biology. Even for those days, few people can have had so much space to develop their own thoughts, unfettered or unmoulded by those of others. And still my good fortune holds, for I now spend a lot of time delving into evolutionary issues. Yet until that subject made a forced entry into my own research territory, I had never actually read a book on evolution since my high school years.² I have always had (or given myself) the freedom, and the time, to ponder — a luxury according to many, a necessity for me. Many young scientists hasten down the path set by their Ph.D. primarily because of security: employment where the next steps are foreknown, and where the competition, the literature, and even the methods are familiar. But the price is often high. Straight-ahead career paths encourage straight-ahead thinking, the all-too-often outcome of which is the not-so-young scientist wishing he or she “just had the time to read and think.” Many of my colleagues imagine they have been caught, like Alice’s Red Queen, in a job where they have to run flat-out to stay in the same place. At times this happens to most of us, but in the longer term the reality is that it can become a habit, where so-called immediate imperatives are allowed to be all-dominating.

I came to work on corals because of two fortunate events. The first was that Terry Done (a colleague at the Australian Institute of Marine Science (AIMS) who also works on corals) started a scuba club at our small rural university, and we found corals where none had been recorded before – at the Solitary Islands off the New South Wales coast, not far north of Sydney. The second was that my Ph.D. turned out to be on an experimental subject where results came thick and fast. I gave a synopsis of my thesis at an International Congress of Entomology in Canberra in 1972 and won a prize, was offered three overseas postdocs (how times have changed), and was

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¹ Why Charlie and why J.E.N.? Well, when I was 6, my teacher nicknamed me “Little Darwin” because I was obsessed with collecting insects and spiders and the like. That soon became the less flattering diminutive “Charlie,” which I’ve been called ever since. But when I went to publish my first paper I discovered that editors don’t like nicknames. So I settled for “J.E.N.” rather than risk a revival of my real name (John) that has always been foreign to me. In retrospect I think this was a bad move because “J.E.N.” sounds formal these days, and rather out of character.

² Curiously for someone nicknamed after Darwin, I did not actually know who he was, nor anything about the subject of evolution, until I was 13. For as long as I can remember I have immersed myself in all things to do with nature, and not unreasonably became very religious, believing that God created it all. The teaching of evolution was banned in Australian schools, and I went to a church school. Then, at that tender age, I read something about “the missing link.” Two traumatic weeks later I emerged from what I can only describe as an emotional collapse, with a hatred of all things to do with my church, school, teachers – the lot. To the end of my secondary schooling I failed most exams, and to this day my first response to new information of any sort is to question it.

advised by the editor of the *Journal of Insect Physiology* to send him my work for publication immediately; otherwise my results would be “stolen.” I accepted the prize and did as the editor bid me do, but I turned down the post-docs. Turning down opportunities of a lifetime – in fact three of them – was not something that students did, even in those days. The harsh words of once-supportive colleagues were still ringing in my ears when I left my old university to take up a post-doc at James Cook University in Townsville (which is about central to the Great Barrier Reef) to work on corals. James Cook University had advertised three times for someone to work on corals who had a Ph.D. and was a scuba diver. I was their only applicant (times have certainly changed) and last hope. I knew next to nothing about corals.

This article is not a biography; I reflect on my own experiences in order to make some points that I think are of general interest. I had dumped an apparently promising career in insect physiology, at that time a field about as big as all the rest of zoology combined, for “a scuba diving holiday,” as my professor described it. What actually happened was that I had listened to myself, and that self knew that I was not an experimentalist who would enjoy a regimented workplace.

What coral research does one do on thousands of kilometers of reef when one knows next to nothing about corals? My plan was to do on reefs what botanists do in forests: describe the communities, work out where they occur, and what the dominant species are – that sort of thing. Enter the word “species,” the word that became central to virtually all my future work. Although James Cook University had a reasonably good reference library for coral taxonomy, I could seldom confidently apply the names I found in these imposing volumes to what could be seen underwater. (And as it turned out, it was many years before I realized the nature, and extent of, the gap between museum-specimen-based coral taxonomy and the realities of the reef.) The essential issue was that as soon as I swam from one environment to another, the species appeared to change, at least a little. I had some knowledge of species in dragonflies, where a minor change in wing venation delineated a different species, or so conventional wisdom then decreed. If such notions were applied to corals, the logical conclusion would be that there are many thousands of species of corals on the Great Barrier Reef, each growing in one specific type of environment, such as a lagoon edge or an outer reef slope (Fig. 1). Nevertheless, the species (if that was the word) that occurred together on the same patch of reef usually appeared more or less distinct. This, and other similar observations, suggested that there was some sort of order, or natural reality, behind the apparent chaos of coral variability as seen underwater.

At this stage I was tempted to continue my work by applying the nearest name from the literature to what seemed to be the species on the reef. Had I had some training in coral taxonomy (or taxonomy of any sort), this is probably what I would have done. As it was, I decided to abandon my research plan, although that seemed a likely path to the ranks of the unemployed – and get to the bottom of this continual (now called intraspecific) variation. Why was it that this variation appeared obvious underwater but was usually ignored by taxonomists? Why did no coral taxonomist ever state how one species could be distinguished from another? Was this taxonomy an end in itself, absolved from responsibility to support other disciplines?

I decided to try to work out precisely how two very well-known corals (I hesitated then to call what I saw “species”), *Pocillopora damicornis* and *Stylophora pistillata*, varied with environment. It was a mixture of laboratory and field work, and the results were, broadly speaking, unbelievable by the standards of any conventional taxonomy (except in plants, but I didn’t think of that at the time). Both species



Figure 1. Bringing taxonomy to the reality of the reef. Most useful taxonomy has been done since the advent of scuba diving, which has allowed coral taxonomists to make careful observations underwater. Great Barrier Reef, Australia (Photo Terry Done).

occurred in a wide range of environments, from the roots of mangroves to wave-hammered reef crests to the deepest depths of outer slopes. When a colony collected from any one of these environmental extremes was compared with a colony from a very different environment, they usually had little or nothing in common. Not only was the growth form different but skeletal details were different also. Yet these details were usually the basis of taxonomic descriptions. It was the lack of gaps in this variation, readily seen underwater (by swimming gradually from one place to another) but also seen under the microscope, that demonstrated links among colonies and indicated the existence (or not) of single species units. OK so far, but this was in stark contrast to what was usually described in taxonomic publications. I decided I didn't like coral taxonomy as a subject and spent most of the following year swimming around reefs, trying to work out what sort of order there was in the apparent chaos of natural variation. Certainly I did not think of *this* as being "taxonomy": I wasn't a "taxonomist." These were people who knew about names and usually (so I then thought) had an awesome knowledge of the detail of skeletal structures. I was just "observing."

That probably would have been the end of this story, had I not had the good fortune to meet two people who reset my stage. The first was "Red" Gilmartin, the first Director of the newly formed AIMS. Apart from offering me a job, Red saw the issues: he said my work *was* taxonomy and that it had to be done before meaningful ecological work on the Great Barrier Reef could be accomplished. AIMS gave me the opportunity to get on with it, and that became the start of the monograph series

Scleractinia of Eastern Australia, undertaken collaboratively with other like-minded field-oriented coral specialists. I reflect now on how much that little bit of insight on Red's part changed the course of my work.

The other person I was fortunate to meet was John Wells, by far the world's most respected coral taxonomist. John well knew that there were problems with the then conventional concept of species in corals, but as he was not a diver he didn't appreciate what the problems were. This came to a crunch at a coral taxonomy workshop held at the Marshall Islands (Fig. 2). We had previously talked about corals at length when I visited John at Cornell University, but at the Marshall Islands we had the opportunity to do more than just talk. I had brought the manuscript of the second volume of *Scleractinia of Eastern Australia* with me in order to get John's comments. He thought the amount of variation my coauthors and I had attributed to several species was "over the top" and singled out *Favites russelli*, one of his own species (and a common one at the Marshall Islands), as a case in point. Armed with hammer, chisel, and plastic laundry basket (the basic tools of the trade), I dived down a reef slope near the laboratory and returned an hour later with about 30 specimens collected at regular depths from the lower slope to the wave-hammered intertidal crest. John and I cleaned them and laid them out in a row on a bench. They made a perfect series, clearly correlated with environment. They convinced John that our observations had, in fact, a sound basis.



Figure 2. Participants Coral Taxonomy Workshop, Marshall Islands, 1976

Top row: Charlie Veron, John Stimson, Paul Jokiel, Gerard Faure, Dennis Devaney, Brian Rosen, Richard Randall

Middle row: Bob Kinzie, Maya Best, Michel Pichon, Jim Maragos, Carden Wallace

Bottom row: Lynton Land, Phil Lamberson, Janet Lamberson, Judy Lang, John Wells, Austin Lamberts

John commented in passing that most coral paleontologists would not hesitate to divide such a series into several genera, and we discussed likely paleontological interpretations had this series of *Favites russelli* been found as a stratigraphically arranged fossil sequence. In all probability, such a sequence would be interpreted as evolutionary change; certainly it would not be attributed to environment: an interesting observation, as valid today as it was then. Such is the continuing gap between coral taxonomy and paleontology. Such comments can be invaluable coming from someone who has the experience to make them. John made another interesting comment a year later, while we were taking a lunch break on a huge Devonian reef about two hours' drive west of where I live. He thought it unlikely that there would ever be a single internationally applicable taxonomic framework for corals. I wish he was still with us – I miss these chats.

This article is about the significant highlights in my work and about what I consider to be turning points. We all have these sort of highlights, and the entry of evolutionary issues (described shortly) is certainly one of them for me. But apart from collecting the insights of people like John Wells and reading a good deal, two things have been especially important to me. The first is the hundreds of conversations I have had with all sorts of people who are willing to share their thoughts with me, irrespective of the subject matter. I am one of those people who store thoughts away, most of which fade, but some pop up in the most unlikely context. It seems to me that humans are good at subconsciously synthesizing information, and that many ideas simply come of their own volition rather than as the intended outcome of planned research. We should always listen to ourselves: intuition, after all, is the outcome of very powerful (cerebral) computers using unimaginably sophisticated programs. The second thing that is important to me is having time to think, even (or especially) if it is, like Winnie the Pooh, thinking about nothing in particular. Powers of deductive logic are probably critical to the work of most scientists, but alas not to me. Give me the soporific combination of a hot sun and a dinghy anchored in calm water on a reef patch, and maybe every so often I'll have a thought that matters.

Fossils and DNA have little in common except that they are linked through our concept of species and of evolutionary change. Or they are thought to be. I have made some personal discoveries here as, no doubt, have dozens of others. I note that palaeontologists love to make pronouncements about genetics, and *vice versa*, yet the jargon is so heavy on both sides that the intended point seems almost never clear to the author, let alone the reader. I note also that if, as rarely happens, a point from one camp *does* manage to infiltrate the other, it does so because of skillful writing, not because of the intrinsic merit of the point. These are unhappy reflections, all the more so because, sandwiched between fossils and DNA, come taxonomy and biogeography, making the issues worse. In general, the dissemination of ideas across distant disciplines is a hazardous undertaking. It usually takes a lot of words; hence "big picture" debates tend to be in books rather than in articles. It also usually invokes the "Scientific American Principle" (as it was once described to me), which states that when an author crosses several discipline boundaries, most readers will give a thumb's-down to the treatment of their own specialty but will probably think the rest is OK.

Being critical is all very well, but many, if not most "big picture" debates are dominated by misunderstanding, or misinterpretation rather than the real issues. At least that was the conclusion I came to while writing *Corals in Space and Time: the Biogeography and Evolution of the Scleractinia*. I read virtually all the relevant

literature of the time (1992-95), not because I wanted to but because I had to because I found good reviews were nonexistent for one subject after another. What I wanted to do was to make a cohesive summary of all research relevant to coral biogeography and evolution and use this as the basis for presenting my own work. This work was multidisciplinary, with the different subjects forming an interlinked network. As it turned out, the task was not the salutary “journey” I had thought it might be. Instead, I found that individual disciplines – paleontology, taxonomy, biological oceanography, ecology, systematics and molecular science – tended to have boundaries, forged by tradition and terminology, which are seldom crossed in meaningful ways. Yet the common subject was “nature” in general and “corals” and “species” in particular; each discipline represented no more than just a different view of the one and same subject.

If I had the space to recall just one incident in retrospect, it would be the following, selected partly because of the subject but also because of the way it happened. The subject, reticulate evolution, I consider to be the most important bit of original work (for want of a better description) I have done. Yet at no stage did this work have an “aim,” and there were never any “materials,” let alone “methods.” To explain, I need to go back about a decade, to a time when I felt confident in my knowledge of the corals of the Central Indo-Pacific (from Australia in the south to Japan in the north). There was some justification for this confidence because, after 20 non-stop years of field and laboratory work, I had studied the corals in most parts of the region and had worked in detail in many. At that time, another field trip to a new location might result in some new (at least new to me) species, but most of what I would see would be all too familiar. I could, more or less, grapple with changes in the appearance of species from one country to the next. That feeling of confident familiarity, however, did not extend to other regions of the Indo-Pacific. If I travelled further afield, east or west, my confidence faltered, not because the corals were different, but because most were neither different nor the same. This became a major issue for me personally: I make mistakes and make “best-guesses,” but I don’t pretend to know what I don’t know. Now, if I ventured into the Central Indian Ocean or Central Pacific, I found myself doubting, with clear justification, different aspects of my own work of so many years. This was serious; I had set out to do my part in what John Wells thought would never be done – the creation of a globally functional taxonomic framework for corals. I thought the taxonomy of corals could be worked out eventually; that species could be described in detail, separated from one another, and mapped. A unified taxonomy, one that took environmental variation into account and one that would support all manner of field and laboratory work, was attainable. Most important of all, this taxonomy would provide the scientific basis for conservation. But, the more I studied the corals of the Central Indo-Pacific (the centre of diversity), the more I doubted the applicability of this work to other parts of the world except in the Caribbean where all species were different. That, at least, was fun. And so, about 10 years ago, I made the decision to bypass the issues rather than confront them. I would not do any more coral taxonomy outside the Central Indo-Pacific.

That was until early one morning (I’m a morning worker) when I got out of bed and went to make a wake-up cup of coffee (as I always do). By the time the jug had boiled, the notion entered my head of its own accord that species were not what I had long assumed them to be. Most were not “natural units” at all; they intergraded geographically, forming patterns of geographic continua. This was a simple, indeed obvious, explanation for what had caused me so much trauma. It made sense of

geographic variation, including problems with taxonomy, synonymies and “fuzzy” distributions. Yet it argued against all current biogeographic theory, in fact the whole neo-Darwinian concept of species, which treated species as units. Then came (while I was still drinking my coffee) the thought that what was observable in geographic space must also apply to evolutionary time. That morning I consulted John Benzie, at that time another colleague at AIMS, who introduced me to what geneticists called “reticulate evolution” and recommended I read Verne Grant’s *Plant Speciation*. I did just that, and found many of my thoughts of the morning clearly set out – for plants.

Reticulate evolution is a paradigm, fundamentally distinct from that of neo-Darwinism (the “neo” meaning the follow-on from Darwin). It offers an alternative view of the nature of species and how species change in space and time. It clearly applies to most corals and (I now believe) to most other “species”, for most species do not form genetically cohesive units. I outline the main points, as applied to corals, below,³ but do so reservedly as I am aware that brief explanations such as this one read like scientific heresy. But, given an hour to present the theory at a conference (as I have done many times), or over a glass of beer (many more times), I get no such reaction – in fact, the very opposite. There are no mysteries about it. The basis is obvious to the point of being undeniable, yet reticulate evolution is either a falsehood, or much of what is generally believed about the nature of most invertebrate and plant species (at least), including their evolution and biogeography, stands on a false premise.

I have described reticulate evolution, as applied to corals, in *Corals in Space and Time* and again, perhaps more clearly, in the third volume of *Corals of the World*. As a concept, it has a lot of development ahead, especially concerning how it interfaces with Darwinian natural selection and the many biogeographic and evolutionary theories that depend on species being units. The bottom line appears to be that natural selection is basically the icing on the cake, icing which comes into existence when, and only when, a species forms a genetically cohesive unit over its whole distribution range. Only then are species what they are generally thought to be: units.

Humans cannot communicate easily in terms of continua. They need to have units of some kind, units with names (such as species names) to which other sorts of information can be attached, e.g., descriptions, maps, ecological attributes, and experimental results. The concept of reticulation makes this difficult. Worse, the concept is destructive, not only of generally accepted neo-Darwinian principles

³ For most marine organisms, ocean currents are the vehicles of larval dispersal and are therefore the pathways of genetic connectivity. These paths repeatedly and continuously change over time, creating changes to the distribution ranges and genetic compositions of species. Geographic space and evolutionary time interact: species diverge, then re-form into different units. For corals, this creates “reticulate” patterns in both geographic space and evolutionary time. In geographic space, species are typically distinct in any single region but lose their identity as taxonomic units over very great distances. When these patterns are envisaged in evolutionary time, species have no time or place of origin and there are no distinctions between sympatric and non-sympatric concepts of origination. Differences between species and subspecies taxonomic levels and between species and “hybrids” are arbitrary and/or unrecognizable. Reticulate evolution is driven by environmental parameters, not biological competition. Rates of evolution and extinction (which occur through fusions as well as terminations of lineages) are similar over long geological intervals. Taxonomic, systematic, and biogeographic concepts of neo-Darwinian and reticulate evolution are mutually exclusive, except where single species form genetically cohesive, reproductively isolated, units. In the latter case, natural selection as the driving force of evolutionary change becomes dominant over environment-driven reticulate change.

embodied in taxonomy, systematics, biogeography, and evolutionary theory, but also of the life-long work of many scientists. So why (I am often asked) do I persist with it? My answer is partly that I would have gone about my own work on corals differently had I known about it. More fundamentally, the concept of reticulation suggests an alternative way of interpreting practically any biological result or observation. It argues that young biologists should think again if they believe they are dealing with any sort of biological unit, for these mostly depend on poorly supported assumptions. I come back to the main point of this article: time to think laterally may be a necessity, not a luxury, if the aim of the work is to get at the truth.

I am also often asked: if reticulation is as widespread as I claim it to be, why is it not generally known or accepted? The answer may be that reticulation is not visible to taxonomists unless the taxonomist works over very large geographic areas as well as in depth. More likely, however, the literature embodying neo-Darwinian thinking (the books alone occupy about three meters of shelf space in my study) offers such a smorgasbord of ideas that none who had received any education in the subject would be likely to question it.

If I may reflect just a little on the foreseeable future, I do not think that reticulate evolution is likely to gain widespread acceptance for the simple reason that natural selection has so much inertia in so many areas and is clearly responsible for the exquisite adaptations we see in nature and presented on TV nature programs. A corollary of this is that cladistics (a supremely logical computer method of phylogenetic analysis and a useful tool in knowing hands) is likely to remain *the* central means of phylogenetic analysis. I find that alarming. It has long been known that cladistics will not work on reticulate systems, but it appears to have been commonly assumed that these systems are unusual or restricted to phylogenies which hybridize. Cladistics packages seldom fail to produce superficially impressive (editor-pleasing) results, yet these results can all too easily displace intuitive thinking. These are, admittedly, idle conjectures. What is not so idle is that we all are guilty, to some degree, of deluding ourselves that we are understanding nature. We should remind ourselves that all we can ever hope to do is make the best of it. The natural world is, and probably always will be, complicated far beyond human understanding.

My concluding “reflections” predictably focus on conservation. When I first worked on the Great Barrier Reef, I always felt a moment of anxiety after rolling backwards off the side of a boat to go for a dive. We all felt that. We waited for the bubbles to clear just to make sure that there wasn’t a big tiger among the sharks that always gathered around. Now, anywhere in the Asian region, I swim long distances over deep water without the slightest concern, for there are virtually no sharks left, big or small. I haven’t even seen big fish in any numbers around an Asian reef in years. The plight of sharks is symptomatic of what is happening to reefs. Destruction through explosive and poison fishing, accompanied by the smashing of the corals in which the fish hide, is now going on at an awesome pace. And now coral reefs are bearing the brunt of global climate change. Having worked in all the major reef regions of the world, my job has become depressing – the last thing I would have once expected.

It was this feeling that prompted Mary Stafford-Smith and me to produce *Corals of the World* (Fig. 3). We hope it can win some hearts as well as minds. We hope it will encourage people of all descriptions to do their part in conserving what is now left. This, more than anything else that I have mentioned in this article, has become what matters.

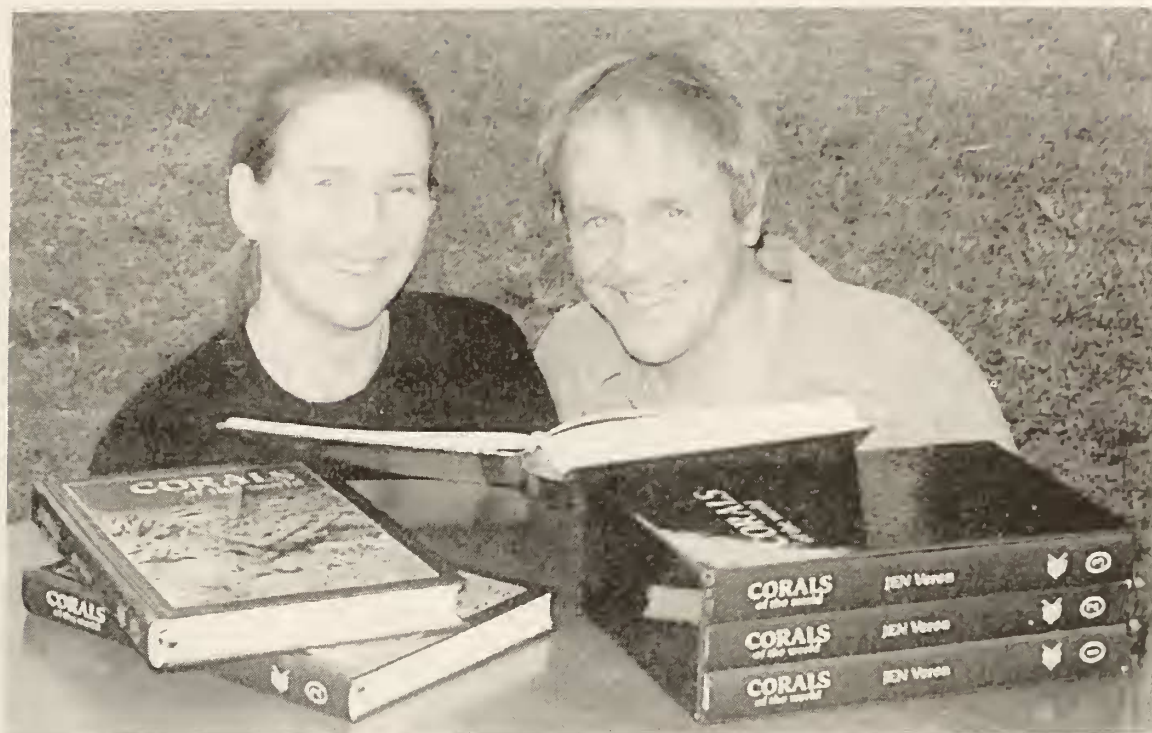


Figure 3. Charlie Veron (author) and Mary Stafford Smith (scientific editor and producer) after the publication of *Corals of the World* in October, 2000. The book was written for the general public and was produced at their home in Townsville, Australia.